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A REDESCRIPTION OF *ENOPLUS GROENLANDICUS* DITLEVSEN, 1926 (NEMATODA: ENOPLIDAE)

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The original description of *Enoplus groenlandicus* Ditlevsen, 1926, was based on two male specimens collected by the Danish Ingolf Expedition in the North Atlantic, one in the Davis Strait and the other south of Iceland. Ditlevsen's description was brief, included limited detail of salient morphological features, and through the intervening years has remained the only published description. Nonetheless, the males of this species usually can be recognized because of the unique bilateral asymmetry of the copulatory apparatus. As pointed out in the original description, one spiculum is approximately 0.5 mm long and nearly straight, while the other is about half as long and more strongly curved. Ditlevsen was of the opinion that the shorter spiculum has been functionally modified so that, together with the gubernacula, it serves as a guiding piece for the longer spiculum.

Numerous specimens made available as a result of the sampling programs conducted by Dr. Howard Sanders of the Woods Hole Oceanographic Institute and Dr. Roland Wigley of the Bureau of Commercial Fisheries, Woods Hole, Massachusetts were tentatively identified as *Enoplus groenlandicus*. This identification has since been confirmed by comparing these specimens with Ditlevsen's type specimens. The new material has enabled us to provide additional information regarding the anatomical features of this nematode, especially the copulatory apparatus, and has provided a basis for a description of the females.

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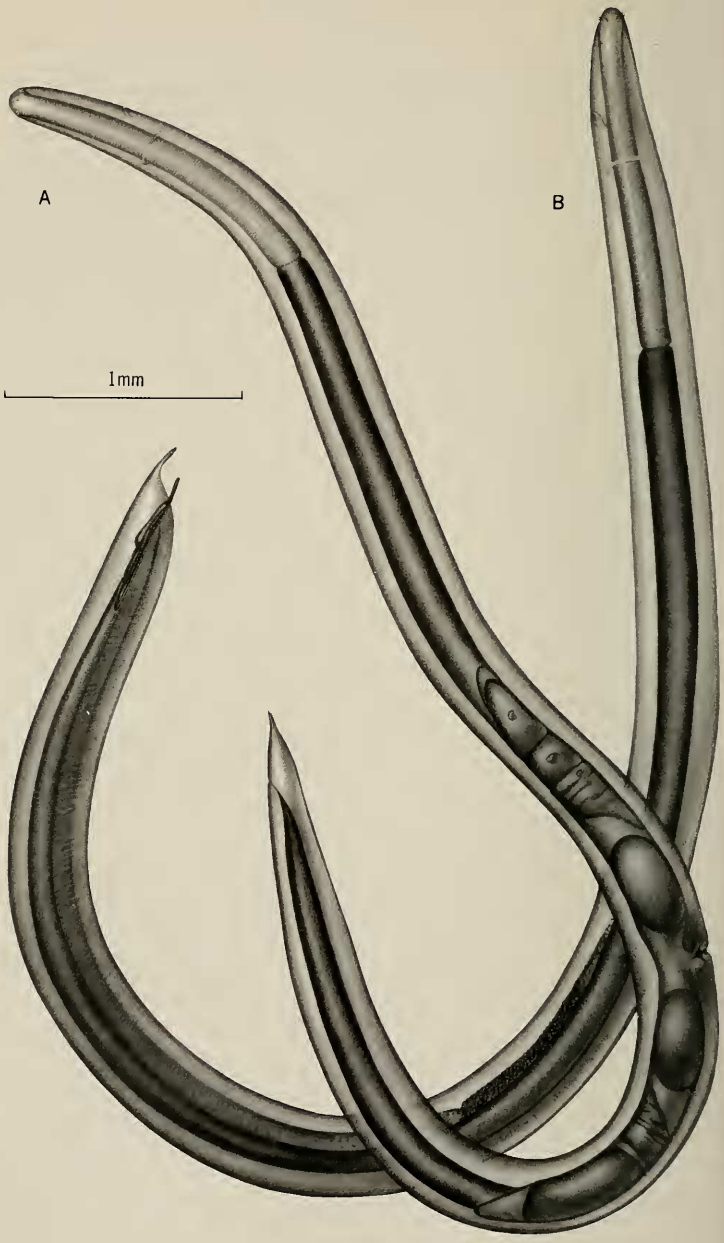
A
B
1mm

The majority of the new specimens used in this study were mounted in anhydrous glycerine. One male specimen (USNM Number 41352) was mounted and cleared in Hoyer's mounting medium for better observation of the copulatory apparatus in lateral view; the posterior end of a second male (USNM 41264) was mounted in glycerine jelly for ventral view of the copulatory apparatus; and the spicula and gubernacula were removed from three males (USNM Numbers 41251, 41252, and 41265) by micro-dissection and mounted in glycerine jelly for detailed study. The heads of two further specimens (USNM Numbers 41266, 41267) were embedded in polyethylene glycol, sectioned at 4 μ and stained by the method of Craig and Wilson (1937).

Dr. Ditlevsen's specimens, one complete male, herein designated the lectotype, and the posterior portion of a second male (paralectotype) had been mounted in glycerine jelly without supports to prevent compression. These specimens have been rehydrated, processed into anhydrous glycerine, and remounted.

Enoplus groenlandicus Ditlevsen, 1926
Figures 1–6

Males—Lectotype and Paralectotype: Zoologiske Museum, Copenhagen, Denmark.

Males—New material: U.S. National Museum of Natural History Numbers 41242–41256; 41258–41260; 41262–41267; 41314; and 41352.

Females—New material: U.S. National Museum of Natural History, Numbers 41295–41313; 41315; 41257; 41261; 41268–41294.

Juveniles—New material: U.S. National Museum of Natural History, Numbers 41316; 41320.

Description: A moderately large nematode. Head bluntly rounded, body tapered in cervical region. Tail basically conical, caudal glands present, slightly convoluted and not extending anterior to junction of mid-gut and rectum. Cells of mid-gut with dark brown pigment. Stoma partially closed by three thin, hyaline flaps. Head with inner circle of six labial papillae and outer circle of 10 cephalic setae. Cervical and somatic setae stout. Amphids lightly cuticularized and difficult to resolve in most specimens, but apparently oval in shape with transverse,

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Fig. 1. *Enoplus groenlandicus*. A, Female (USNM 41247). B, Male (USNM 41276).

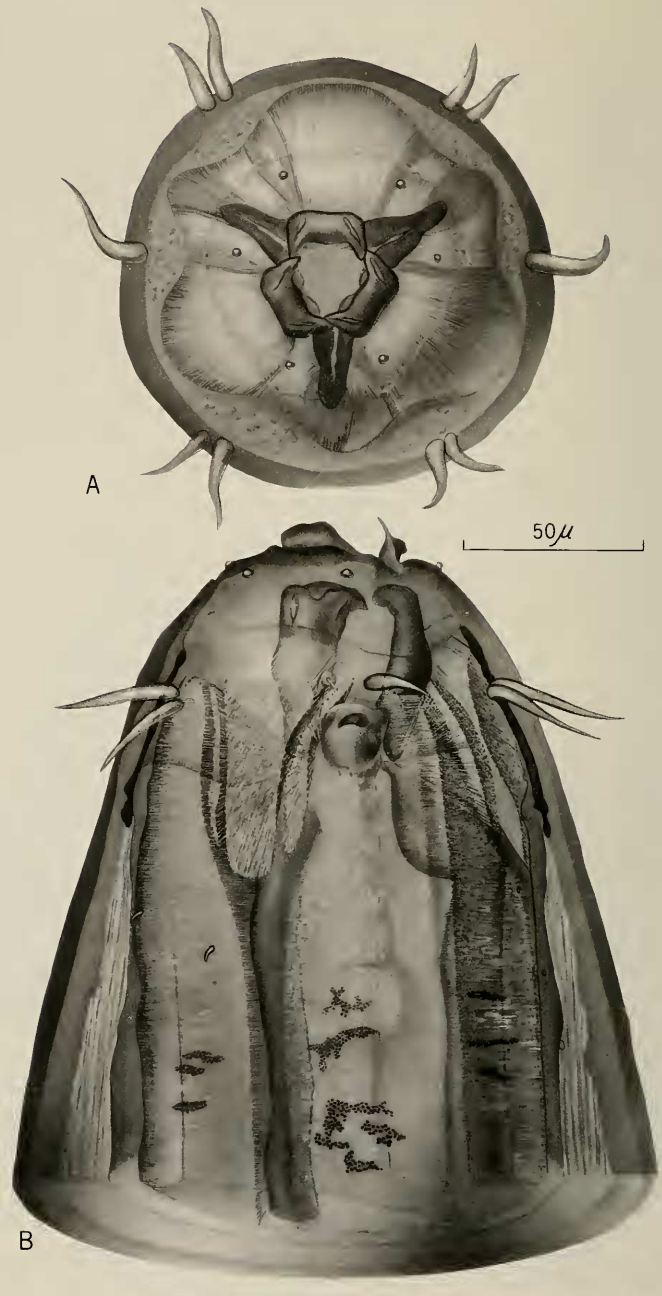

FIG. 2. *Enoplus groenlandicus*. A, Face view of male (USNM 41263). B, Lateral view of male head (USNM 41244).

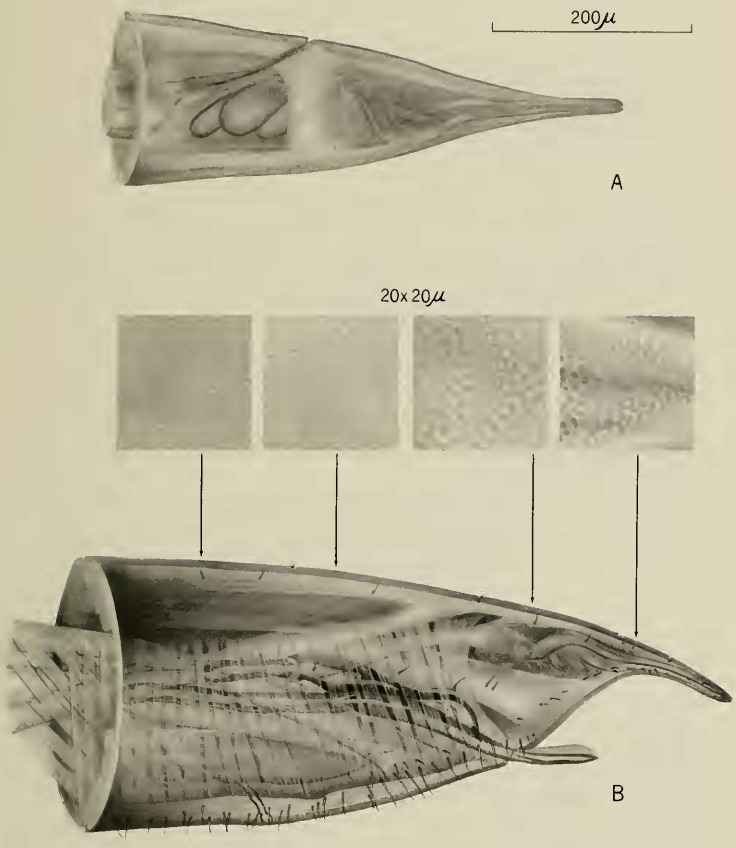

Fig. 3. *Enoplus groenlandicus.* A, Lateral view of female tail (USNM 41276). B, Lateral view of male tail (USNM 41247). Photographs of cuticular punctations taken in region of the lateral chord of the same male at levels indicated by the arrows.

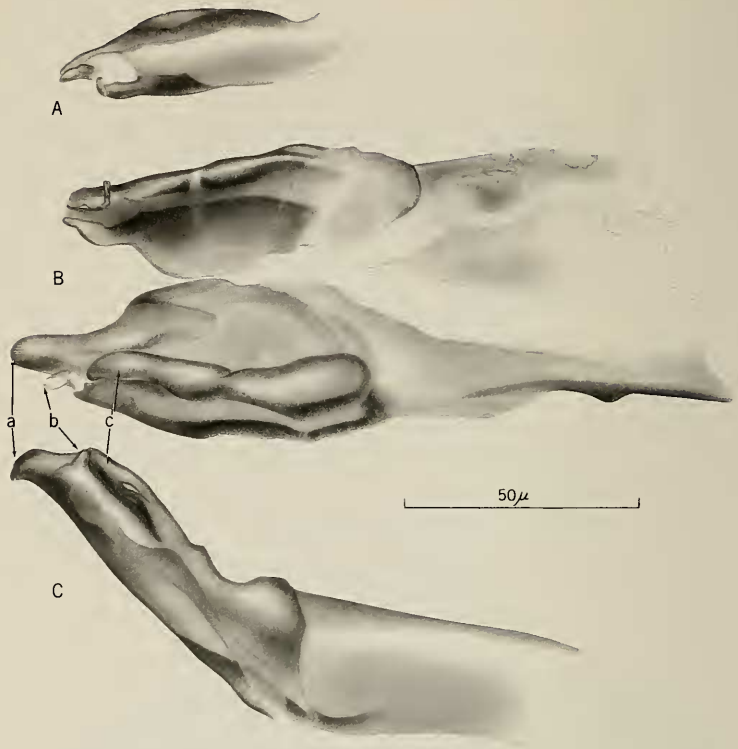

Fig. 4. *Enoplus groenlandicus.* A, Lateral view of right side of gubernacular complex (USNM 41352). B, Ventral view of gubernaculum with right component above and left component below. Note posterior (a), median (b), and anterior (c) lobes of left component (USNM 41265). C, Lateral view of left side of gubernacular complex (USNM 41352).

external slitlike orifice (Fig. 2B). Cephalic capsule present, but lightly cuticularized and difficult to resolve even in optical sections; cephalic suture present but faint (Fig. 2B). Cuticle posterior to cephalic suture with punctations up to nearly 2.0 μ in diameter on neck and anal regions,

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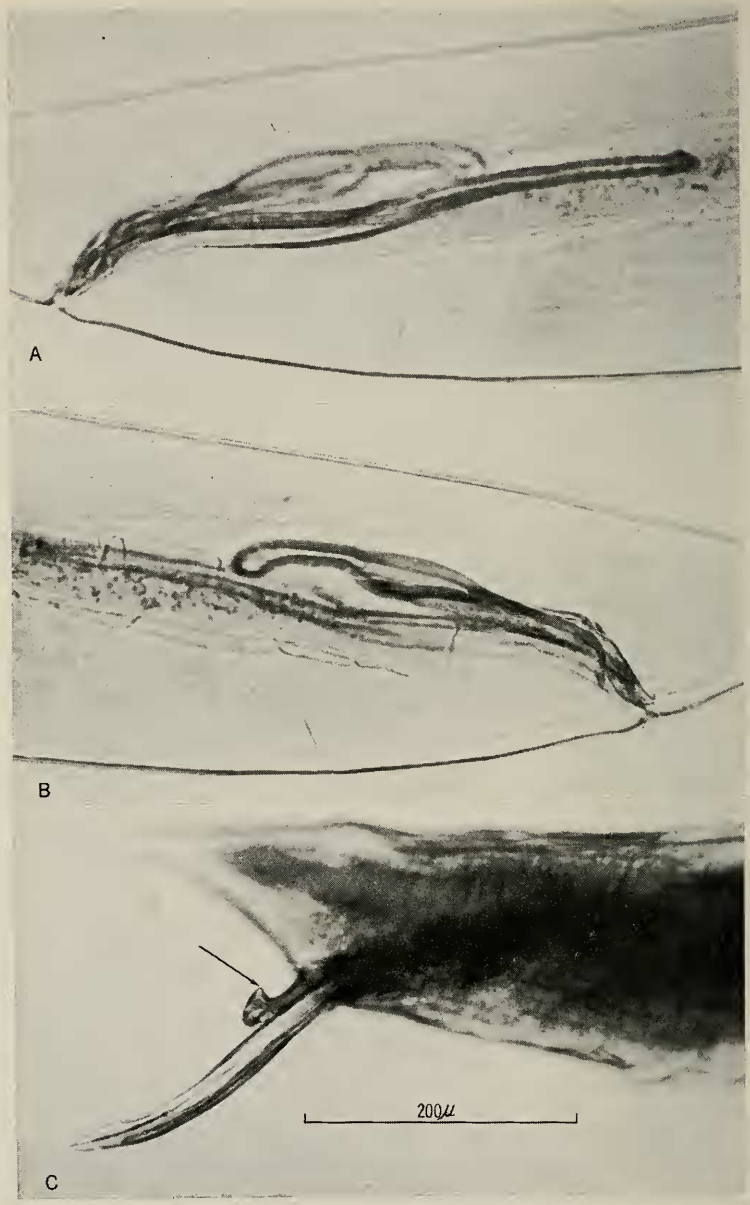
Fig. 5. *Enoplus groenlandicus.* A, Lateral view of right (retracted position) spiculum (USNM 41252). B, Lateral view of left (retracted position) spiculum (USNM 41265). C, Ventral view of left (protruded position) spiculum (USNM 41265). Arrows indicate each medial process.


A
B
C
200μ


A
B
200μ
C

less than 1.0 μ on mid-body regions and terminal portion of tail. Larger punctations with darker core (Fig. 3B).

Stoma with three prominent mandibles, each bifurcated to form two medially directed teeth. Radii of stoma in lip region with longitudinal striations. Esophagus cylindrical but slightly tapered and with diffuse pigmentation; ocelli absent. Excretory pore, terminal duct and ampulla usually, but not always distinct; ventral gland encircling base of esophagus.

Females—Females as above; ovaries paired and reflexed. Tail conical, tapered uniformly on dorsal and ventral sides (Fig. 3A).

Males—Subventral copulatory supplements setiform and numerous. Ventromedian supplement short, cylindrical and straight to slightly arched anteriad (Fig. 3B). Tail tapered, but more so on ventral side, and with slender, cylindrical, terminal process (Fig. 3B). Testes typically opposed and outstretched: sperm small, round. Vas deferens with narrow anterior portion and wider, muscular posterior portion. Right spiculum long and narrow; proximal one-half nearly straight; distal half with narrow velum bearing transverse striations (Fig. 3B). Distal end curved with tip directed caudoventrally when retracted (Fig. 6A), but curved with tip directed caudally when extended (Figs. 3B and 6C). Left spiculum in lateral view when retracted or resting (Figs. 3B, 5B and 6B) with proximal and distal ends directed ventrally; proximal third of spiculum relatively slender, becoming wider in mid-region and then tapering to acute distal end; process present on medial side of spiculum near distal end (Figs. 5B, 5C and 6C. Arrow). Left spiculum rotated 90° when extended with distal tip directed toward median longitudinal plane, and medial process directed dorsally (Fig. 5C and 6C). Both spicula devoid of semicircular plates. Gubernacular complex, comprised of two heavily cuticularized, right and left components, joined by a lightly cuticularized membrane. Left portion of gubernaculum (Figs. 4B and 4C) with three posteriorly directed lobes (a, b, c). Terminal or most posterior lobe (a) with longitudinal striations: middle, posteriorly directed lobe (b) shorter and possibly a sensory receptor; anterior lobe (c) arising from ventral surface of gubernaculum and arched laterally at distal extremity. Right half of gubernaculum shorter and apparently without comparable lobes (Figs. 4A and 4B).

Discussion: Enoplus groenlandicus can be distinguished from other species of this genus by the combined features of no eyespots; a short, rather straight, cylindrical ventromedian supplement; and no semicircular plates on the spicula. Furthermore, it is unique in having

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Fig. 6. *Enoplus groenlandicus*, male tail. A and B, Same specimen (USNM 41352) right (A) and left (B) lateral views. C, Specimen with spicula partially protruded (USNM 41258). Arrow indicates medial process.

Table 1.

	Number Measurements	Range	Mean	Standard Deviation	Standard Error
Total length ♂♂ (mm)*	8	8.29–9.93	8.99	0.58	0.21
Total length ♀♀ (mm)	10	9.09–11.12	10.00	0.60	0.19
Dist.—ex. pore ♂♂**	8	347–486	423	52.1	18.4
Dist.—ex. pore ♀♀	10	351–545	452	51.0	16.1
Length esoph. ♂♂ (mm)	8	1.31–1.50	1.40	0.08	0.03
Length esoph. ♀♀ (mm)	10	1.39–1.60	1.48	0.05	0.02
Distance to vulva (mm)	10	5.00–5.74	5.38	0.27	0.08
Tail length ♂♂	8	229.0–271.0	256.0	16.0	6.0
Tail length ♀♀	10	274.0–330.0	304.0	19.0	6.0
Head diameter ♂♂	8	97.0–108.0	100.3	4.1	1.5
Head diameter ♀♀	10	101.0–115.0	106.6	4.2	1.3
Length ceph setae ♂♂	8	31.0–36.0	33.5	1.8	0.6
Length ceph setae ♀♀	10	28.0–36.0	32.0	2.7	0.9
Dorsal mandible length ♂♂	8	46.4–50.5	48.7	1.51	0.54
Dorsal mandible length ♀♀	10	51.5–56.7	53.3	1.63	0.51
Maximum body diameter ♂♂	8	228.0–385.0	336.0	35.6	12.6
Maximum body diameter ♀♀	10	319.0–385.0	355.2	20.6	6.5
Anal body diameter ♂♂	8	153.0–163.0	157.0	3.4	1.2
Anal body diameter ♀♀	10	132.0–153.0	142.0	7.1	2.2
Length vms ♂♂***	8	41.7–57.2	51.1	4.8	1.7
Distance vms-anus ♂♂	8	198.0–247.0	228.0	20.0	7.1
Right spiculum ♂♂	8	483.0–548.0	522.0	24.1	8.5
Left spiculum ♂♂	10	275.0–315.0	299.0	16.1	5.1

* All measurements in micra except where milimeters are indicated.
** Dist.—ex. pore = distance from anterior end of head to level of excretory pore.
*** VMS = ventromedian copulatory supplement.

spicula that differ from one another in size and shape. It is of interest to note that the right spicula are dissimilar to the left in the males of *Mesacanthion diplechma* Southern 1914 (Enoplidae) and have at least a superficial resemblance to those of *Enoplus groenlandicus*. This similarity is here regarded as an example of convergent evolution since, in the case of the *Mesacanthion* species, the right spiculum is shorter than the left. Within the same superfamily, Enoploidea, other examples of dissimilar spicula may be found, such as in the case of *Pseudocella wieseri* Hope, 1967 and *P. panamaense* Allgen 1947.

The postulation by Ditlevsen that the left spiculum, together with the gubernacular complex, serves to guide the right spiculum is apparently not correct since in our material we have found specimens with both spicula protruding from the cloaca side by side and, therefore, it is likely that each has a similar function.

TABLE 2.

Ship	Cruise	Station	Date	Latiude N	Longitude W	Corrected Depth (Meters)	Sediment	♂♂	♀♀	Juve-niles
ALBATROSS III	101	11	22 Aug. 1957	41°49.0′	69°05.0′	181	Sandy silt-clay	1	0 –	0
ALBATROSS III	101	51	23 Aug. 1957	41°39.0′	68°50.0′	151	Very fine sand	0	3 (4)*	0
ATLANTIS I	277	D-1	23 May 1962	39°54.5′	70°35.0′	466–508	———	8	26(49)	0
ATLANTIS II	12	73	25 Aug. 1964	39°46.5′	70°43.3′	1330–1470	———	1	0 –	0
ATLANTIS II	24	126	24 Aug. 1966	39°37.0′ to 39°37.5′	66°47.0′ to 66°44.0′	3806	———	11	18(34)	4
DELAWARE	10	114A	29 June 1961	43°09.0′	69°00.0′	189	Fine sand	0	1 (7)	0
GOSNOLD	49	2089	8 Aug. 1964	37°11.0′	74°26.0′	1105	Clayey silt	0	0 –	1
GOSNOLD	49	2101	9 Sept. 1964	37°55.4′	73°54.0′	880	Clayey silt	1	0 –	0
GOSNOLD	49	2138	17 Aug. 1964	39°55.0′	70°51.9′	500	Sandy silt	0	1 (0)	0
DELAWARE	7	31A	16 June 1962	40°57.0′	70°30.0′	49	Fine sand	1	0 –	0

* Total number of ova for all females in parentheses.

A further peculiarity lies in the fact that the left spiculum appears to rotate 90° as it is extruded, thus presenting a very different appearance in lateral view. In this situation the medial process is directed dorsally and the distal extremity is directed medially (Figs. 5C and 6C). If but a single male specimen with the left spiculum extruded were available for identification, it might easily be misidentified as a member of another species. The right spiculum too, has a different appearance when extruded, as in this situation it arches dorsally (Fig. 3B). However, it is not clear whether it rotates or bends. The functional significance of this rotation, and possible bending of the right spiculum, is not understood, but it may serve to anchor the female to the male during copulation.

The new collections of *Enoplus groenlandicus* extend our knowledge of their distribution. Whereas the species had not been collected previously from further south than 61°28′N, it is now known to be distributed at least as far south as 37°11′N and at depths of 49 meters on the continental shelf to 3800 meters on the abyssal plain. The extreme depths suggest that pressure itself is not a limiting factor in the distribution of this species and supports a similar conclusion reached by Sanders, Hessler, and Hampson (1965) regarding invertebrates in general.

Temperature, on the other hand, may be important. A large number of temperature determinations have been provided by the National Oceanographic Data Center for all seasons of the year at localities and depths comparable to the two stations (D1 and 126) from which the largest numbers of specimens were obtained. The seasonal temperature variation at the deeper locations ranges from 2.2° to 3.5° C and at the shallower from 4.3° to 8.9° C. Thus, the known temperature range for *E. groenlandicus* is approximately 2.0° to 9.0° C. A few specimens have also been collected on the continental shelf, but in these instances they have been north of 41°N: samples examined to date from the continental shelf south of 41°N have not yielded representatives of this species. It may be that this species can exist in colder waters only, and that its southward distribution on the continental shelf might, therefore, be limited by the warmer waters of the Gulf Stream.

It is also possible that certain properties of sediments are important in regulating nematode distribution, as has been suggested by Wieser (1969). Unfortunately, in this study there were too few stations with adequate sediment data to draw correlations between numbers of specimens and sediment characteristics.

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